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The genus Radula in Macaronesia

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Seven species of *Radula* are confirmed to occur in Macaronesia: *R. wichurae*, *R. lindenbergiana*, *R. nudicaulis*, *R. holtii*, *R. jonesii*, *R. aquilegia*, and *R. carringtonii*. For each species descriptions, distribution, and other notes are provided. Six species are illustrated. All reports of *R. complanata* appear to be based on misidentifications and it has therefore been excluded from the Macaronesian flora.

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Подтверждено, что в Макаронезии встречаются семь видов Radula: R. wichurae, R. Lindenbergiana, R. nudicaulis, R. holtii, R. jonesii, R. aquilegia, и R. carringtonii. Для каждого вида приводятся описания, распространение и другие заметки. Проиллюстрированы шесть видов. По-видимому все регистрации R. complanata основаны на ложной идентификации и, следовательно, она исключена из флоры Макронезии.

During our work on the bryophyte flora of the Canary Islands it appeared that several *Radula* specimens could not be named satisfactorily with the commonly used handbooks (i.a., Maevicar 1926, Müller 1951/1957). Especially the taxonomy of *R. holtii* Spruce and *R. carringtonii* Jack was confusing. Having experienced the difficulties in applying *Radula* names ourselves, we guessed that many literature records would be based upon misidentifications. We therefore began to revise *Radula* for the Canary Islands. However, it soon turned out to be necessary to include the specimens from the Azores, Madeira, and the atlantic part of SW Europe. This paper presents the results of a revision of the Macaronesian *Radula* species. It provides an identification key, descriptions, and illustrations of most species.

Key to the species

1. At least some leaves with apical margin of both lobes distinctly bordered with 1–3 rows of small hyaline cells..... *Radula wichurae*
*. All leaves with the lobes unbordered 2
2. Lobules distinctly ampliate, caducous leaves often present in the older parts..... *Radula nudicaulis*
*. Lobules not ampliate, leaves not caducous 3
3. Leaves gemmiferous, often strongly so .... *Radula lindenbergiana*
*. Leaves never gemmiferous 4
4. Plants paroecious, mostly with perianths, these more than 4 times longer than wide; androecia inconspicuous, often hidden by the leaves; leaf cells thin-walled, without trigones..... 5
*. Plants dioecious; perianths rare, less than 4 times longer than wide; androecia in conspicuous spikes; leaf cells thick-walled with distinct trigones..... 6
5. Stem in cross-section with cortical cell walls thickened, distinctly differentiated from the thin walled medullary cells, perianth mouth smooth .... *Radula holtii*
*. Stem in cross-section with cortical cells undifferentiated from the medullary cells, all with large trigones, perianth mouth distinctly lobed *Radula jonesii*

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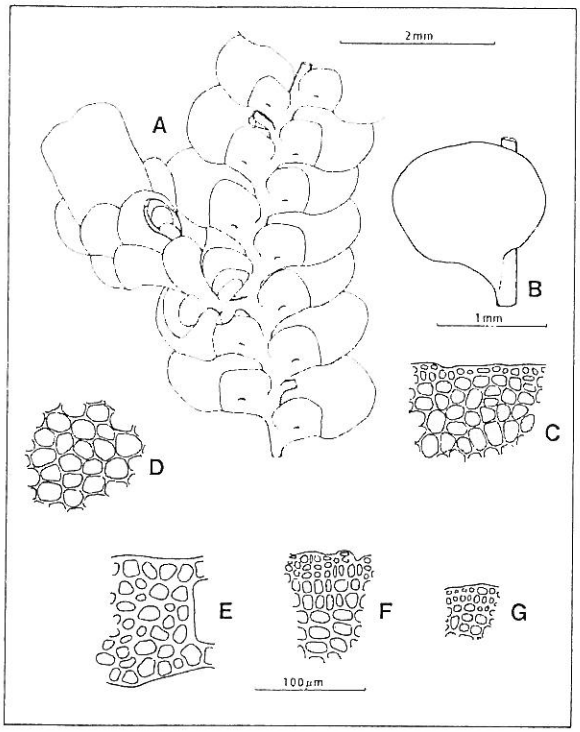

Fig. 1. *R. wichurae* Steph. A. Ventral aspect of shoot with perianth; B. Lobe; C. Marginal leaf cells; D. Median leaf cells; E. Cross-section of main stem; F. Cells of perianth mouth; G. Marginal cells of lobule. A-D, F, G from Madeira, Porto Santo, leg. Johnson, herb. Mitten. E. from Canary Islands, Tenerife, leg. Dirkse no. RIN 003959.

6. Leaves concave, lobule rectangular, carinal region inflated, the keel often strongly arched .... *Radula aquilegia*

*. Leaves nearly always flat, lobule quadrate, flat, the keel more or less straight..... *Radula carringtonii*

Description of species

Radula wichurae Steph. (Spec. Hep. 4: 168. 1910.) Fig. 1.

Plants olive-green to brownish with age. *Stem* 15–30 mm long, 0.15–0.18 mm in diameter, with *leaves* 2.6–3.2 mm wide, more or less regularly pinnately branched; cross-section of stem 7–8 cells thick, both cortical and medullary cells thick-walled. Lobes contiguous to imbricate, slightly concave, ovate, 1.5–1.9 mm long, 1.3–1.7 mm wide, apex rounded, the base rounded and extending beyond the stem, not auriculate, insertion curved. Median cells 20–25 × 15–19 µm, marginal hyaline cells 6–10 × 6–7 µm, rather thin-walled without trigones, more rarely thick-walled with trigones. Lobules more or less ovate, 0.6–0.7 mm long, 0.5–0.6 mm wide, apex rounded to obtuse, base rounded, the base occupying 1/2 its width, covering the stem 1/2 to the entire distance of the stem width, not auriculate, insertion substraight, keel incurved to substraight, 0.5–0.6 mm long, rhizoid initial region slightly convex. *Dioecious. Androecium* terminal or intercalary on branches, with 6–12 pairs of densely imbricate bracts, keel strongly arched. *Gynoecium* terminal on branch, without or with 1 innovation, bract lobe resembling leaf-lobe, bract lobule, ovate, keel more or less straight. *Perianth* 2.4 mm long and 1.4 mm wide at the mouth, strongly compressed, keeled along the margins, otherwise unistratose. Mature *sporophyte* not seen. The margin of the leaf lobes, lobules and bracts and also the mouth of the perianth with 1–3 rows of small hyaline cells.

Diagnostic characters

1. Lobules more or less ovate. 2. Apical margin of lobe and lobule distinctly bordered with small hyaline cells. 3. Keel incurved to substraight.

Habitat

On rocks and trunks of trees. Mostly in very sheltered localities: evergreen forest on steep northern slopes or deep ravines; periodically wetted volcanic rocks on steep northern slopes. Alt. 500–750 m.

Distribution

Az: Sao Miguel, Santa Maria, Flores, Faial, Corvo, Graciosa. Reported from Pico and Sao Jorge (Sjögren 1978) and Terceira (Buch and Persson 1941).
Ma: Madeira, Porto Santo.
Ca: Tenerife
R. wichurae is endemic to Macaronesia (Castle 1960).

The small hyaline cells are mostly very distinct, but may sometimes only be present on a few leaves. We always succeeded in finding them, although Castle (1960) mentions two collections from the Azores made by Allorge in 1937 (Ribeira da Cruz, Flores no. 23 and Ribeira Quente, Sao Miguel no. 24) in which the hyaline cells are completely lacking. We have not seen these specimens among Allorge's collections in PC. But in YU there is a small duplicate, named *R. wichurae* and made by Castle from a collection of Allorge from Ribeira da Cruz. Although it has no number we believe that it is a duplicate from no. 23. Castle's remark applies here in that it has the lobes unbordered. However, in our opinion the specimen belongs to *R. carringtonii*.

Selected specimens examined

Type: Azores, leg. Wichura (G no. 024297)

AZORES: Corvo; Pico, Agosthino, 1 Nov 1954 (S);

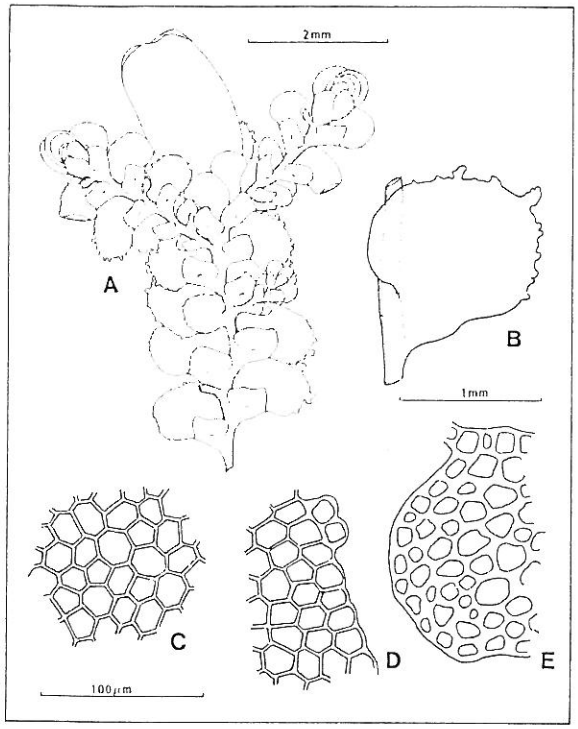

Fig. 2. *R. lindenbergiana* Gott. ex Hartm. f. A. Ventral aspect of shoot with perianth; B. Lobe; C. Median leaf cells; D. Marginal leaf cells; E. Cross-section of main stem. All from Gomera, Roque Zarzita, leg. Schwab, 24 Apr 1984.

Ribeira das Rocinhas, Agosthino, 11 Nov 1954 (S): Faial; Oberhalb Flamengos, Eggers Az 8/15 (hb. Eggers); Caldera, Persson 1937 (S): Flores; Ponta Delgada, Trelease, Jul 1894, ex hb. Underwood (NY); Fajasinha, Allorge Iter Azoricum Rad 13 (PC): Graciosa; s.l. Carreiro, Jul 1903 (YU); Pico Timao, Sjögren G8/21 (UPSV): Sao Miguel; Lagoa do Congro, Allorge Iter Azoricum Rad 8 (PC, YU, UPSV); Lagoa do Furnas, Eggers Az2/28 (hb. Eggers); Terra Garda, Persson, 20 Mar 1937, ex hb. Mauno (H): Santa Maria; Bananeiras, Allorge Iter Azoricum Rad 14 (PC).

CANARY ISLANDS: Tenerife; Anaga Mountains, Pico de Limante, Hallingbäck 3 Dec 1976 (S).

MADEIRA: Madeira; Funchal, Bornmüller, Flora Exsiccata Madeirensis 183 (S); Porto do Moniz, Ribeira do Tristoo, Costa 96 (S); Funchal, Curralinho, Bornmüller 183, holotype of R. ovata, ex hb. H. Reimers (YU): Porto Santo; s.l., Johnson (NY); Pico da Gandaia, Costa 324+325 (UPSV).

Radula lindenbergiana Gott. ex Hartm. f. (Handbok Skand. Fl. ed. 9. 2: 98. 1864.) Fig. 2.

Plants green, rarely brown with age. *Stem* 10–25 (30) mm long, 0.16–0.20 mm in diameter, with *leaves* 1.6–2.8 mm wide, irregularly pinnately branched; cross-section of stem 7–10 cells thick, both cortical and medullary cells thick-walled. Lobes imbricate, slightly concave, 0.7–1.1 mm long and 0.6–0.9 mm wide, apex rounded, the base rounded, not auriculate, extending beyond the stem, insertion substraight. Discoid marginal gemmae rarely absent on the apical margins. Median cells 16–23 (26) × 12–20 (23) µm, marginal cells 12–18 × 12–16 µm, cells thin-walled without or with minute trigones. Lobules subquadrate to rectangular, nearly flat, 0.4–0.7 mm long, 0.3–0.6 mm wide, apex mostly narrowly rounded and somewhat apiculate, especially on branch leaves, base rounded, the base occupying 1/3–1/2 the width, covering the stem 1/3–1/2 (3/4) the stem width, not auriculate, insertion substraight, keel substraight to slightly arched, 0.4–0.6 mm long, not decurrent, rhizoid initial region slightly convex. *Dioecious. Androecium* terminal or intercalar on stem or main branch, with 8–16 (20) pairs of densely imbricate bracts, the keel strongly arched. *Gynoecium* terminal on the stem or main branch, with 1–2 innovations, bract lobe resembling the lobe, bract lobule rectangular, keel straight. *Perianth* up to 2.0 mm long and 1.4 mm wide at the mouth, rectangular to oblong, compressed, unistratose throughout except for the keeled margin or bistratose at base with bistratose strands extending upwards to 2/5 its length. *Capsule* oval, brown. *Spores* 26–30 µm in diameter, greenish, finely echinate; elaters bispiral, brownish, 6–7 µm wide.

Diagnostic characters

1. Leaves gemmiferous, often strongly so. 2. Leaf cells thin-walled, without or with minute trigones. 3. Apex of lobule narrowly rounded, often somewhat apiculate. 4. Androecia in long distinct spikes.

Habitat

Very common on all kind of trees and rocks in forests, but also on trees along roads and on exposed rocks in open ravines. Alt: 300–1500 m.

Distribution

Az: Sao Miguel, Santa Maria, Sao Jorge, Faial. Reported from Terceira and Pico (Sjögren 1978).
Ma: Madeira.
Ca: Tenerife, Gran Canaria, Lanzarote, Palma, Hierro, Gomera. Reported from Fuerteventura by Malme (1988).
CV: Sao Nicolao, Sao Tiago.
R. lindenbergiana is mainly distributed on the N. hemisphere (Schuster 1980): Europe, N. Russia, E. & SE. Asia, SW. Asia, N. Africa, Macaronesia, N. America, Greenland. There is a disjunction in S. Africa.

R. lindenbergiana is nearly always easy to identify by

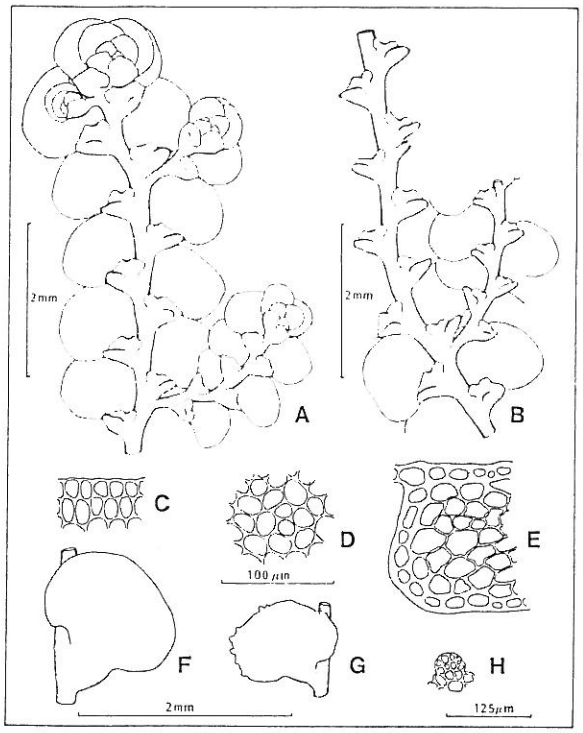

Fig. 3. *R. nudicaulis* Steph. A. Ventral aspect of mature shoot; B. Ventral aspect of shoot with caducous leaves; C. Marginal leaf cells; D. Median leaf cells; E. Cross-section of main stem; F. Lobe; G; Lobe showing marginal gemmae; H. Marginal gemma. All from Madeira, leg. Schwab no. SN 133.

being strongly gemmiferous. Rarely specimens occur in which gemmae are very sparse or completely absent. These could be mistaken for *R. carringtonii*, but may be separated from this species by the following combination of characters: leaf cells thin-walled, lobule often longer than broad, especially on branches and weaker stems, apex of lobule slightly acuminate.

Selected specimens examined

AZORES: Faial; Conceisa pres Horta, Allorge, 30 Jun 1937 (PC): Graciosa; Furna, Sjögren G4/17, G4/18 (UPSV): Santa Maria; Meio Molho, Allorge Iter Azoricum Rad 1 (PC); Vila do Porto, Allorge, 23 Jun 1937 (PC): Sao Jorge; Calheta, Allorge Iter Azoricum Rad 18 (PC): Sao Miguel; Ponta Delgada, Armitage, 4 Mar 1930 (GL); Furnas, Schwab SN 79 (hb. Schwab), Eggers Az 1/8 (hb. Eggers); Ribeira de Guillerme, Allorge Iter Azoricum Rad 20 (PC).

CANARY ISLANDS: Gran Canaria; Jafira, A. Carter Cook 654 (NY, E, S); Monte Barranco Guiniguada, Bornmüller, 1 Apr 1901 (D); El Palmar, Koppe, 13 Apr 1977(1) (D): Gomera; Las Rosas, During 80378 (hb. During); Roque Zarzita, Schwab, 24 Apr 1984 (hb. Schwab); Oberhalb Hermigua, Eggers C13/42 (hb. Eggers): Hierro; El Golfo, Bines BH84 (E): Lanzarote; Near las Nieves, During 78–31 (hb. During): Palma; Mirka bei Santa Cruz, Dull 017586 (D); W slopes of Cumbre Nueva, Long 563 (E); Los Tilos, Hallingbäck, 2 Apr 1974 (hb. Hallingbäck): Tenerife; Aguamansa, Crundwell 115 & 120 (GL); Teno Gebirge, Schwab SN 165 & SN 169 (hb. Schwab); Taganana, Arnell, 19 Mar 1958 (S); Orotava, Koppe, 15 Mar 1975(3) (D).

CAPE VERDE ISLANDS: Sao Nicolau; Cuckaco, Byström 1959 (S); Mount Vermelha, Byström, May 1959 (S): Sao Tiago; Serra Malagueta, Byström, 31 Mar 1959 (S).

MADEIRA: Madeira; Ecumiada Gebirge, Friedländer, May 1963 (S); s.l., Johnson 1861 hb. Mitten (NY); Ribeiro Frio, Arts 16147, 16156, 16164 (hb. Arts); Rabacal, Hillebrand 653 (FR).

Radula nudicaulis Steph. (Spec. Hep. 4: 174. 1910.) Fig. 3.

Plants brown to red-brown with age. *Stem* 20–30(40) mm long, 0.16–0.20 mm in diameter, red-brown and very glossy when dry, with *leaves* 2.4–2.8 mm wide; often regularly pinnately branched; cross-section of stem 9–11 cells thick, cortical cells thick-walled, brown, medullary cells thin-walled, hyaline. Leaf lobes contiguous to imbricate, slightly concave, ovate, often somewhat falcate, 1.1–1.4 mm long, 0.9–1.2 mm wide, apex rounded to obtuse, the base rounded and extending beyond the stem, sometimes slightly auriculate, insertion substraight. Median leaf cells 17–21 × 15–19 µm, marginal cells 11–15 × 11–13 µm, mostly thin-walled with trigones. Leaf lobes often caducous, at least on some stems with gemmae on the older leaves. Lobules quadrate, 0.4–0.6 mm long, 0.4–0.5 mm wide, apex rounded to obtuse, front margin sinuate at the middle and appressed to the leaf lobe, base ampliate, occupying 1/3 its width, covering the stem 1/3–1/2 the stem width, not auriculate, insertion substraight, keel straight to arched, 0.4–0.5 mm long, not decurrent, carinal region strongly inflated. *Sex organs* not seen.

Diagnostic characters

1. Plants large, often somewhat shrunken when dry. 2. Lobules quadrate with the base distinctly ampliate. 3. Carinal region strongly inflated. 4. Stem in cross-section with cortical cells distinctly differentiated from the medullary cells. 5. Leaves often caducous.

Habitat

On trunks of trees and on rocks in forests and woodlands, mostly above 900 m.

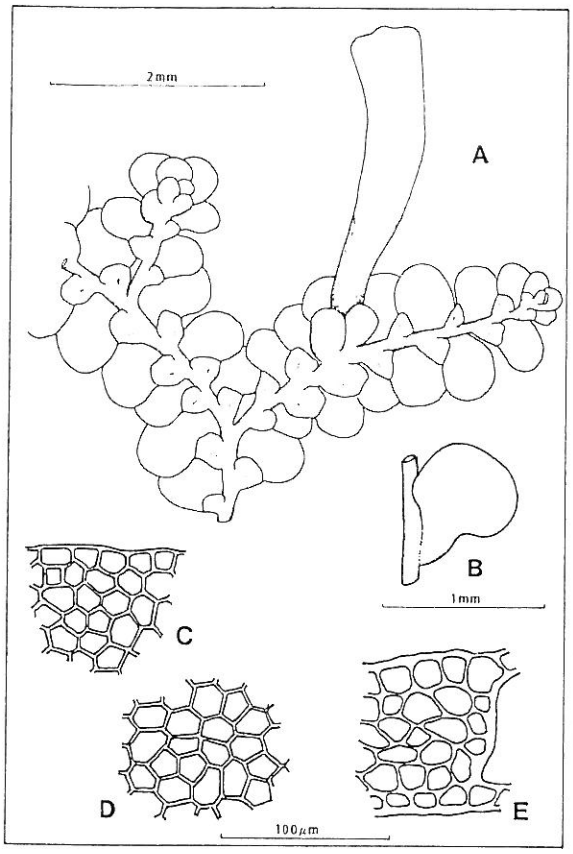

Fig. 4. *R. holtii* Spruce. A. Ventral aspect of shoot with perianth; B. Lobe; C. Marginal leaf cells; D. Median leaf cells; E. Cross-section of main stem. All from: Madeira, Rabacal, 14 May 1952, leg. Een & Persson.

Distribution

Az: Sao Miguel, Faial, Pico.
Ma: Madeira
According to Yamada (1982) *R. nudicaulis* occurs in Brazil, Bolivia, Columbia, and Macaronesia.

R. nudicaulis var. *delicatula* Allorge (Rev. Bryol. Lichén. 19:106. 1950). *Plants* distinctly smaller. *Stem* 10–15 mm long, more branched, branches short and slender, with *leaves* up to 2.0 mm wide; lobes and lobules smaller, but hardly differing in shape from *R. nudicaulis* s.str.

We have seen only one collection made by Allorge in 1937 (Sao Miguel, Pico Verde no. 10) and identified by Castle as *R. aquilegia*, which strikingly resembles *R. nudicaulis* var. *delicatula*. However in this variety the lobes are less rounded and more elliptic. Unfortunately, the type of var. *delicatula* was not available so we had to rely upon Allorge's protologue and pictures.

Although *R. nudicaulis* is very distinct from all other Macaronesian *Radula* species it has often been confused with *R. aquilegia*. The diagnostic characters, however, easily separate it from this species. Caducous leaves are nearly always present in the older parts of the plant. Some old leaves may show proliferous regenerations before they fall off. These gemmae-like structures do not represent true gemmae as thought of by Jans (1979), because they have no particular shape and are only formed on old leaves. We have seen one collection made by Persson in 1937 from Pico, which resembles *R. nudicaulis*, but differs from it in having the base of the lobe not crossing the stem and with the cells thin-walled without trigones. These characters point to *R. holstiana* Steph., a very variable, monoecious, widely distributed African species, which might occur in Macaronesia. However, since the collection is small and without gametoecia we prefer to keep the identification preliminary.

Selected specimens examined

Type: Brasilia, Serra do Itatiaia, leg. E. Ule 436 (G no. 20986)

— AZORES: Faial; Caldeira, Eggers Az 9/50, Az 9/49, Az 9/11 (hb. Eggers): Pico; Lagoa do Capitao, Eggers Az 12/17 (hb. Eggers): Sao Miguel; Lagoa do Fogo, Eggers Az 6/15 (hb. Eggers), Schwab SN 133 (D, hb. Schwab); Pico da Vara, Allorge Iter Azoricum, 2 Jun 1937 (S); Salto do Cavalo, Eggers Az 4/3 (hb. Eggers).
— MADEIRA: Madeira; Ribeira do Passo, Nobrega & Persson, 1 Jul 1952 (S); Casa das Queimadas, Schwab SN 236 (D, hb. Schwab); Ribeiro Frio, oberhalb der Forellenteiche, Koppe, 6 Apr 1970 (1) (D); Levada de Portela, Eggers MD 3/24 (hb. Eggers); Paul da Serra, Rabacal, Arts 16108 (hb. Arts).

Radula holtii Spruce (Journ. Bot. 25: 209. 1887.) Fig. 4.

Plants green to olive-green, becoming olive-green with age. *Stem* 15–20 mm long, 0.09–0.13 mm in diameter, with *leaves* 1.7–2.2 mm wide, irregularly pinnately branched; cross-section of stem 5–7 cells thick, cortical cells thick-walled, brown, medullary cells thin-walled, hyaline. Lobes imbricate, flat to slightly concave, ovate, 0.8–1.0 mm long, 0.7–0.8 mm wide, often slightly falcate, apex rounded, the base rounded, not auriculate, covering the stem 1/2–2/3 the stem width, never extending beyond the stem; insertion substraight. Median cells 19–23 × 17–21 µm, marginal cells 10–15 × 10–13 µm, thin walled without trigones. Lobules subquadrate, 0.25–0.35 mm long, 0.30–0.40 mm wide, apex rounded to obtuse, base substraight to slightly rounded, the base occupying 1/4 its width, covering the stem 1/5 the stem width, not auriculate, insertion substraight, keel mostly distinctly arched, 0.30–0.35 mm long, rhizoid initial region convex. *Paroecious. Androecium* 1–2 pairs of un-

modified leaves below the female bracts, antheridia fugacious. *Gynoecium* terminal on branch or stem with 1–2 innovations, which are often again fertile, bract lobe resembling the lobe, bract lobule ovate to more or less rectangular, keel straight. *Perianth* 2.0–2.5 mm long, 0.5–0.6 mm wide at the mouth, bistratose below with bistratose strands upwards, tubular in the lower half, subcompressed above, compressed at the mouth only. *Capsule* oval, brown. *Spores* 19–22 µm in diameter, green, smooth; elaters bispiral, light brown 5–6 µm wide.

Diagnostic characters

1. Paroecious. 2. Leaf cells thin walled. 3. Stem in cross-section with cortical cells distinctly differentiated from the medullary cells. 4. Perianth trumpet shaped.

Habitat

On trunks or leaves of evergreen trees in dense forest. On wet rocks in very sheltered localities in dense forest; sometimes epiphyllic on fronds of ferns or large mosses. Alt: 500–1100 m.

Distribution

Az: Faial. Reported from Sao Miguel, Sao Jorge, and Pico (Sjögren 1978).
Ma: Madeira.
Ca: Tenerife.
Outside Macaronesia *R. holtii* is confined to the W and SW extremities of Europe (Smith 1990).

R. holtii was described by Spruce (1887) as dioecious. However, the male plants which Spruce (1887) described represent *R. carringtonii* with which *R. holtii* was intermingled at the locus classicus (Torc Cascade, Ireland). Also the illustrations of androecia by Macvicar (1926), and Castle (1967) represent male plants of *R. carringtonii*. This has lead to much confusion, because, as was already mentioned by Jones (1977), *R. holtii* is paroecious. Androecia of *R. holtii* are hard to find, because androecial bracts do not differ from normal leaves and the antheridia are fugacious. Antheridia are, however, always to be found by carefully dissecting the top of well-grown innovations, immediately below the archegonium.

Collections of *R. carringtonii*, with the leaf lobes not crossing the stem were mostly named *R. holtii*, because when identified with Macvicar (1926) they key out as *R. holtii*. Proper identification of these plants, even when perianths are lacking is possible by looking for antheridia or, which is often less time consuming, making a cross-section of the stem.

We have not seen the holotype mentioned by Grolle (1976). However we have seen three isotypes distributed by Carrington and Pearson as Hep. Brit. Exs. no 273. Only one (MANCH 50550) contains a few fragments of *R. holtii*. The other two only contain *R. lindenbergiana* or *R. complanata*. Since the type collection was a mixture of 2 or 3 species it is very likely that other collections distributed as no. 273 do not contain *R. holtii*.

Selected specimens examined

Isotype: Ireland: Killarney; Torc Waterfall, leg. Holt no. 273 ex hb. C. Bailey (MANCH 50550).

AZORES: Faial; Cabeco dos Trinta, Sjögren Ac/F3 (UPSV).

CANARY ISLANDS: Tenerife; Anaga Mountains, N of Pico de Limante, Hallingbäck, 13 Dec 1976 (S); Anaga Mountains, Roque de Anambra, Bouman 88197 (hb. Bouman).

MADEIRA: Madeira; Rabacal, Een & Persson, 14 May 1952 (S); Ribeiro Frio, Punto do Suna, Nobrega & Persson, 9 Jul 1952 (S).

IRELAND: Killarney; Torc Cascade, Schiffner Hepaticae Europaeae Exsiccatae 490a, b (MANCH, U).

PORTUGAL: Minho; Serra do Gerês, Parque Tude de Sousa, Tavares (LISU 148071): Caldas, Machado KK937 ex hb. Nicholson (MANCH).

Radula jonesii Bouman, Dirkse & Yamada (J. Bryol. 15: 161. 1988), ill: Bouman et al. (1988).

Plants medium-sized, dark- to olive-green. *Stem* 10–15 mm long, 0.07–0.12 mm im diameter, irregularly pinnately branched, branches 2–5 mm long, ca 0.08 mm in diameter. Stem 5–7 cells thick. Epidermal walls dark brown, as large as the lighter coloured medullary cells, both in cross-section thick-walled with large trigones.

Lobes moderately imbricate, flat to slightly concave, narrowly ovate to ovate (rarely suborbicular), 0.7–0.9 mm long, 0.5–0.6 mm wide, apex obtuse (rarely broadly rounded), not incurved, basal margins arched, not auriculate at bases, usually covering 1/2–2/3 of the stem width (never extending beyond the stem); insertions substraight. Median cells irregularly hexagonal to shortly rectangular, 14–18 × 9–11 µm, marginal cells 10–13 × 7–9 µm. Cell walls thin, evenly thickened, without trigones. Lobules flattened, appressed to the lobe, subquadrate, apex bluntly acute, often somewhat apiculate, apical and frontal margins more or less straight. Base straight to slightly convex, not auriculate, normally not extending beyond the stem mid-line, leaving a leaf-free area of three rows of ventral epidermal stem cells. Insertion substraight, 0.13–0.16 mm long. Keel more or less straight, 0.23–0.28 mm long, not decurrent, sinus wide. Rhizoid-initial region slightly convex.

Paroecious. Androecia (4–6), on stem or branch,

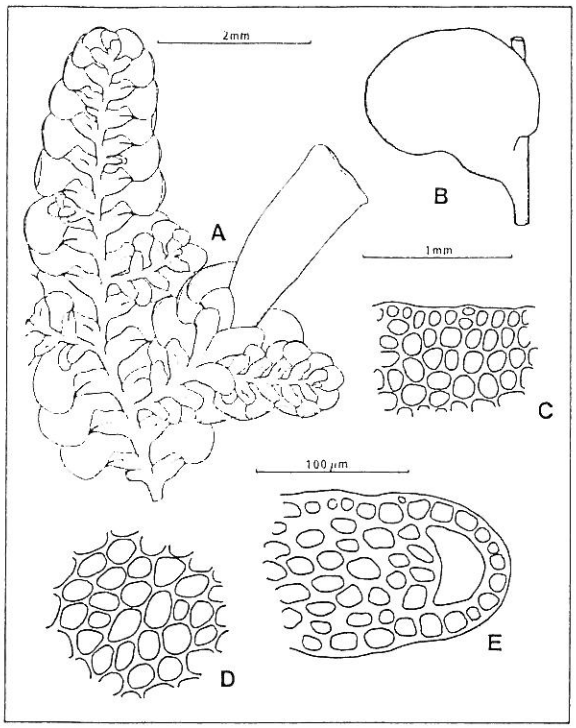

Fig. 5. *R. aquilegia* (Hook. f. et Tayl.) Gott. et al. A. Ventral aspect of shoot with perianth; B. Lobe; C. Marginal leaf cells; D. Median leaf cells; E. Cross-section of main stem. All from Azores, Terceira, leg. Crundwell 846.

bracts unequally bilobed, imbricate, saccate, keel strongly convex. *Gynoecium* terminal on branch or stem with 1–2 subgynoecial innovations. Bracts unequally bilobed. Bract lobe 1.0–1.3 mm long, 0.6–0.7 mm wide, oblong to ovate with widely rounded apex. Bract lobule 0.6–0.8 mm long 0.25–0.30 mm wide, almost rectangular, apex subacute to acutely rounded, keel sinuate.

Perianth long, cylindric, to 2.5 mm long, 0.2 mm wide at base, gradually widening to 0.6 mm at the mouth. Basal part tubular with bistratose strands extending towards the unistratose middle part. Upper part unistratose throughout and only slightly flattened. The mouth with irregular lobes.

Capsule ovoid. Spores green, 18–22 µm in diameter. Exine brownish, slightly roughened. No means of vegetative propagation seen.

Diagnostic characters

1. Paroecious, dark- to olive-green plants. 2. Arched bases of leaf lobes never crossing the stem. 3. Uniformly thin leaf cell walls. 4. Perianth cylindrical, irregularly lobed at mouth. 5. Epidermal stem cells in cross-section with large trigones and thickened walls, not sharply differentiated from the medullary cells.

Habitat

On wet, shaded rocks in laurel forest on steep N slope. Alt. 700–800 m. Associated species: *Lejeunea ecklo-niana, Radula wichurae, R. lindenbergiana, R. carring-tonii, Harpalejeunea ovata, Drepanolejeunea hamatifo-lia, Marsupella emarginata, Trichostomum brachydon-tium,* and *Hypnum cupressiforme.* Epiphytic on Madeira.

Distribution

Ca: Tenerife; Anaga Peninsula, Pico de Limante.
Ma: Madeira; Faldas do Pico Jorge, Ribeira Bonito, Madre da Levada de S. Jorge, Sergio & Nobrega 6202 & 6214.

R. jonesii has not yet been found elsewhere.

Selected specimens (see: Bouman et al. 1988).

Radula aquilegia (Hook. f. et Tayl.) Gott. et al. (Syn. Hep.: 260. 1845.). Fig. 5.

Plants olive-green, to red-brown with age. *Stem* 15–25 (30) mm long, 0.12–0.16 mm in diameter, with *leaves* 1.9–2.3 mm wide, more or less regularly pinnately branched; cross-section of stem 6–8 cells thick, both cortical and medullary cells thick-walled. Lobes imbricate, concave, ovate, sometimes slightly falcate, 0.6–1.1 mm long, 0.5–0.9 mm wide, apex rounded, the base rounded, not auriculate, mostly extending beyond the stem, insertion slightly curved. Median leaf cells 21–23 × 17–21 µm, marginal cells 8–13 × 8–10 µm, cell walls thickened with distinct trigones. Lobules rectangular, 0.4–0.6 mm long, 0.3–0.4 mm wide, apex rounded, front margin nearly parallel to the keel and appressed to the lobe, base slightly rounded, the base occupying 1/4 the stem, covering the stem 1/4–1/3 the stem width, not auriculate, insertion substraight, keel arched, often strongly so, 0.5–0.6 mm long, not decurrent, carinal region inflated. *Dioecious, androecium* terminal or intercalary on branches, with 4–8(12) pairs of densely imbricate bracts, the keel strongly arched. *Gynoecium* terminal on a short branch, usually with 1, rarely 2 innovations, bract lobe resembling the lobe, bract lobule rectangular, keel incurved. *Perianth* to 3 mm long and 1 mm wide at the mouth, unistratose throughout, rarely bistratose at base with bistratose strands extending upwards to 1/3 its length. *Capsule* oval, red-brown. *Spores* 44–50 µm in diameter, pale yellowish green, translucent, finely echinate; elaters bispiral, light brown, 8–9 µm wide.

Diagnostic characters

1. Leaves distinctly concave. 2. Lobule rectangular, with the front margin nearly parallel to the keel. 3. Keel arched, often strongly so. 4. Carinal region inflated.

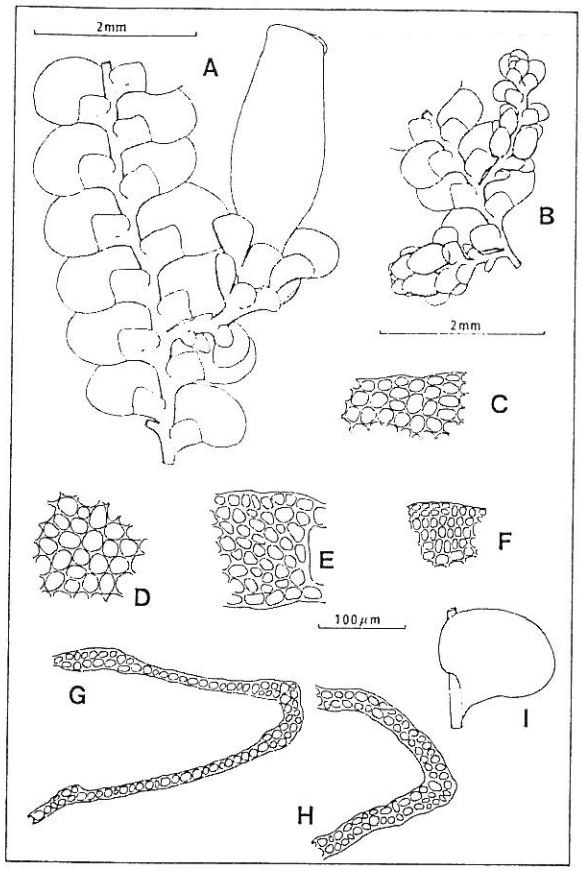

Fig. 6. *R. carringtonii* Jack. A. Ventral aspect of shoot with perianth; B. Ventral aspect of shoot with androecia; C. Marginal leaf cells; D. Median leaf cells; E. Cross-section of main stem; F. Cells of perianth mouth; G. Cross-section of perianth at 2/5 from base; H. Cross-section of perianth at base; I. Lobe. A-H from Madeira, Lamaceiros, leg. Johnson, herb. Mitten. I from Azores, Faial, Caldera, leg. Persson 1937.

Habitat

On stem and leaves of trees in dense forests. Also on sheltered rocks in dense forest on N slopes. Alt. 200–800 m.

Distribution

Az: Sao Miguel, Sao Jorge, Flores, Terceira, Faial, Pico.
Ma: Madeira
Ca: Tenerife. The records from Gran Canaria by Koppe and Düll (1986) appear to be based upon specimens which represent *Scapania compacta* (Roth) Dum.

According to Smith (1990), *R. aquilegia* is restricted to Macaronesia and the W and SW extremities of Europe, with a large disjunction in the Himalayas.

Selected specimens examined

Isolectotype ?: Ireland: Bantry, leg. Hutchins (BM ex K. no. 63)

AZORES: Faial; Cabezo dos Trinta, Schwab SN 445 (hb. Schwab); Caldeira, Eggers Az 9/7, Az 9/59 (hb. Eggers): Flores; Fajâsinha, Allorge Iter Azoricum s.n. (PC); Ribeira da Cruz, Allorge Iter Azoricum Rad 15 (PC); Pico S. Francisco, Allorge, 17 Jul 1937 (PC): Sao Jorge; Calheta et Topo, Allorge Iter Azoricum Rad 2 (PC): Sao Miguel; Pico Verdhe, Allorge, 2 Jun 1937 (PC); Salto do Cavalo, Schwab SN 169a, SN 169b, SN 192 (hb. Schwab); Lagoa do Congro, Eggers Az 5/23, Az 5/13 (hb. Eggers): Terceira; Angra do Heroismo, Crundwell 846 (D).

CANARY ISLANDS: Tenerife; Las Mercedes, Arnell, 18 Mar 1958 (S); La Laguna, Las Mercedes, Hallingbäck, 19 Dec 1973 (hb. Hallingbäck); Anaga Mountains, Roque de Anambra, Dirkse no. 006135 (hb. Dirkse).

MADEIRA: Madeira: Ribeira Frio, Koppe, 31 Mar 1970(5b) (D); Borda de Bonito, Costa 99 (S); Rabacal, Een & Persson, 14 May 1952 (S); s.n., Johnson, hb. Mitten (NY).

Radula carringtonii Jack (Flora 64; 385. 1881.) Fig. 6.

Plants brown with age. *Stem* 20–30(35) mm long, 0.10–0.16 mm in diameter, with *leaves* 2.1–2.7 mm wide, irregularly pinnately branched; cross-section of stem 7–8 cells thick, both cortical and medullary cells thick-walled. Lobes contiguous to imbricate, slightly concave, ovate, 1.1–1.5(1.9) mm long, 0.9–1.2(1.5) mm wide, apex rounded, the base rounded, not auriculate, mostly extending beyond the stem, insertion curved. Median leaf cells 21–25 × 19–22 µm, marginal cells 11–16 × 11–13 µm, cell walls mostly thickened with distinct trigones, more rarely rather thin-walled with small trigones. Lobules more or less quadrate, nearly flat, 0.45–0.70 mm long, 0.45–0.65 mm wide, rounded at apex, apical margin more or less parallel to the stem, base rounded, the base occupying 2/5 the width, covering the stem 1/2 the stem width, not auriculate, insertion substraight; keel substraight sometimes slightly incurved, 0.4–0.6 mm long, not decurrent, rhizoid initial region slightly convex. *Dioecious. Androecium* terminal or intercalary on short branches, with 4–6 pairs of densely imbricate bracts, the keel strongly arched. *Gynoecium* terminal on a short branch, without- or with 1 innovation, bract lobe resembling the lobe, bract lobule more or less ovate, keel straight. *Perianth* to 3 mm long and 1.1 mm wide at the mouth, unistratose throughout or bistratose at base with bistratose strands extending upwards to 2/5 its length. *Capsule* oval, brown. *Spores* 30–38 µm in diameter, pale yellowish, translucent,

finely echinate; elaters bispiral, yellowish brown, 6 µm wide.

Diagnostic characters

1. Leaves slightly concave. 2. Lobules more or less quadrate, flat, with rounded apex. 3. Leaf cells thick-walled with distinct trigones.

Habitat

On stem of trees in dense forest, also on shaded, periodically wetted rocks in dense forest. Alt. 200–800 m.

Distribution

Az: Sao Miguel, Faial, Flores, Pico, Santa Maria. Reported from Terceira and Sao Jorge (Sjögren 1978).
Ma: Madeira.
Ca: Tenerife
Confined to Scotland, Ireland and Macaronesia (Smith 1990).

Although most specimens have thick-walled leaf cells with distinct trigones, sometimes specimens occur with rather thin-walled cells and less marked trigones. These could be taken for a non-gemmiferous *R. lindenbergiana*. However in *R. carringtonii* always some leaves can be found in which the cells are thick-walled and trigonous, especially at the apical leaf margins. In small forms of *R. carringtonii* the lobule may be rectangular as in *R. aquilegia*. These forms differ from the latter species in having the keel of the lobule flat and substraight.

Selected specimens examined

Type: Ireland, Killarney, leg. Carrington June 1861 (G no. 024292)

AZORES: Faial; Zabezo das Trinta, Schwab SN 435 (hb. Schwab); Misterias, Allorge Iter Azoricum Rad 12 (PC); Caldera, Persson 1937 Hep. Azorici (S): Flores; Pico de S. Franciscâo, Allorge Iter Azoricum Rad 4 (PC); Ribeira da Fazenda, Allorge, 12 Jul 1937 (PC); Zwischen Furna do Frei Matias und Cabeco Gordo, Eggers Az 11/52 (hb. Eggers): Pico; Furnas do Pico, Allorge Iter Azoricum Rad 17 (PC); Lagoa do Capitao, Eggers Az 12/16 (hb. Eggers): Santa Maria; Pico Alto, Allorge, 20 Jun 1937 (PC); San Laurenzo, Allorge, 21 Jun 1937 (PC): Sao Miguel; Furnas, Cedercreutz, Plantae Azoricae 1938 (H); Pico da Cruz, Ade 25 May 1935 (D).

CANARY ISLANDS: Tenerife; Anaga Mountains, Pico de Limante, Bouman 87076 (hb. Bouman).

MADEIRA: Madeira; Lamaceiros, Johnson 1859, hb. Mitten (NY); Ribeira Frio, Pickering, 20 Feb 1964 (S), Koppe, 9 Apr 1970 (D); Montado da Chaô das Feiteiras, Een & Persson, 30 Apr 1952 (S); Ribeira dos Touros, Hillebrand 538 (FR); Between Casa las Quiemadas and Calderas Verde, Arts 16237 (hb. Arts).

IRELAND: Killarney, Schiffner, Hepaticae Europaeae Exsiccatae 487 a,b,c (U); Killarney, Torc Cascade, Schiffner, Hepaticae Europaeae Exsiccatae 490 c (U, MANCH).

Excluded species

Radula complanata (L.) Dum. has been reported many times from Macaronesia (Eggers 1982). However, since we did not see a single *R. lindenbergiana*-like collection which was monoecious, *R. complanata* should be excluded from the bryophyte flora of Macaronesia.

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